THE SUBSPECIES OF LUPINUS CULBERTSONII AND L. CUSICKII (LEGUMINOSAE)

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Polymorphy is especially common in the lupines of the western United States and has long created confusion among taxonomists. By detailed morphological, ecological, and chemical means, small groups of complexes of lupines have been studied by various monographers in efforts to gain insight into the biology of the genus. The following taxonomic treatment of five taxa is an excerpt from an extensive biosystematic study of over 80 described western United States perennial, herbaceous, caespitose lupines (Cox, 1972a). Since these lupines are of special interest in population variation studies, the taxonomic treatments are published here to facilitate later reference to these taxa. On a delineation of morphological traits (Cox, 1972a), it is hypothesized that *Lupinus cusickii* and other related small caespitose lupines are allied to plants that are morphologically similar to *L. culbertsonii*.

The taxonomy is based on comparisons of seed proteins and alkaloids (to be published elsewhere), as well as morphological and field studies conducted during several growing seasons. Chromosome numbers were reported by Cox (1972b). For brevity, complete exsiccatae are not cited here. The following herbaria generously loaned specimens for study: CAS, DS, GH, ISC, JEPS, MIN, MO, NY, ORE, OSC, POM, RM, RSA, UC, UMO, US, WILLU, WIS, WS.

KEY TO THE TAXA

1.a. Peduncles surpassing the foliage; plants of the Sierra Nevada, Cali-
fornia
b. Peduncles not surpassing the foliage; plants of eastern Oregon and
adjacent Idaho
2.a. Stems with 1-2 nodes, branching infrequently; peduncles 8.5-16.0
cm long; along the Kaweah River, Tulare Co.; at 2440-2650 m.
1a. L. culbertsonii subsp. culbertsonii
b. Stems with 3-6 nodes, branching frequently; peduncles 1.5-8.0 cm
long; from Mono Co. to Tulare Co.; at 2900–3500 m.
1b. L. culbertsonii subsp. hypolasius
3.a. Racemes completely surpassed by the foliage; flowers 8.5-9.0 mm
long 2a. <i>L. cusickii</i> subsp. cusickii
b. Racemes not completely surpassed by the foliage; flowers 9.5-11.5
mm long
4.a. Plants less than 12 cm tall; leaflets 5–6; stipules 4–5 mm long.
2c. L. cusickii subsp. brachypodus
b. Plants usually 12–15 cm tall; leaflets 6–7; stipules 10–15 mm long;

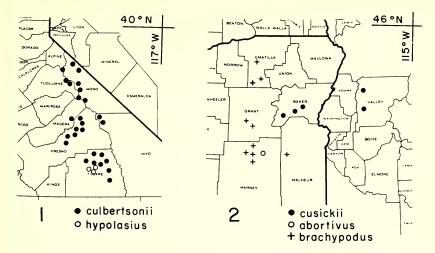
Stinkingwater Mt., Harney Co., Ore. 2b. L. cusickii subsp. abortivus

LUPINUS CULBERTSONII Greene subsp. CULBERTSONII, Leafl. Bot. Observ. Crit. 1:73. 1904. TYPE: United States: California: Tulare Co.: Kaweah River, South Fork, *Culbertson 4475* (Holotype: ND; Isotypes: MO, NY, POM, UC). — L. lepidus var. culbertsonii (Greene) C. P. Sm., Bull. Torrey Bot. Club 51:304. 1924.

Plants perennial, foliage in basal clumps from slender woody caudex, branching not prominent in most specimens; stems 15-36 cm tall, 1.5-2.5 mm in diameter, strigose or with sparsely spreading pilose-hirsute pubescence to 2 mm long, acaulescent to 2 cauline nodes; cauline petioles 3–9 cm long; basal petioles 3–8 cm long; stipules 6–9 mm long, adnate to petioles 4-5 mm; leaflets 6-7, oblanceolate, obtuse-rounded to short mucronate, the largest 1.3–2.8 cm long, 5.5–7.0 mm wide, length to width ratio 2.28-4.36(5.09), av 3.31, sparse sericeous to short pilosevillous, pubescence 1.5–2.0 mm long; peduncles well exceeding the foliage, 8.5-16.0 cm long; racemes 4-9 cm long, 2.5-2.7 cm in diameter, 6-8 verticils, 5-12 mm apart; flowers blue with white to yellow sulcus, 10.2-11.5 mm long; bracts caducous, 4.0-4.5 mm long, subulate, pilose-sericeous: pedicels 2.0-2.7 mm long; calyx bilabiate, upper-lip 4.2-5.0 mm long, bilobed, notch 1.8-2.7 mm deep, lower-lip 4.8-5.8 mm long, tip entire to slightly serrate, lips connate 1.1-1.5 mm, bracteoles persistent, 0.5-1.8 mm long, attached at the sinus to 0.8 mm back, pilose-sericeous, pubescence to 1.5 mm long; banner suborbicular, glabrous, 10.0-10.5 mm long, 7.8-9.0 mm wide, length to width ratio 1.11-1.31, av 1.24, reflexed at or above the midpoint, reflexed to appressed ratio (0.8) 0.92-1.00, angle 121–150°; wings 9.0–10.0 mm long, 5.3–5.8 mm wide, length to width ratio 1.67-1.82, av 1.75; keel 2.8-3.5 mm wide at the widest point, angle 98-106°, sparsely ciliated along the upper-outer half, most dense near the acumen; ovules 4; pods 13-15 mm long, 4.5-5.0 mm wide, subappressed, sericeous-villous; seeds 4, 3.0-3.5 mm long, 2.8-3.0 mm wide, 1.2-1.6 mm thick, beige-tan with darker brown mottlings; flowers late in July–early August; 2n = 48 (Cox 1972b); (fig. 3).

DISTRIBUTION: This infrequently collected subspecies is endemic to a very small region along the South Fork of the Kaweah River, Kaweah Meadows and Hockett Meadows in Tulare Co., California (fig. 1). It occurs at elevations of 2440–2650 meters.

Plants are morphologically somewhat intermediate between Lupinus culbertsonii subsp. hypolasius and L. sellulus. Flower size and shape, as well as lax, verticillate racemes are traits shared with subsp. hypolasius. However, subsp. culbertsonii lacks the profuse branching and general spreading pilose to hirsute pubescence common in subsp. hypolasius. Instead, it has sparse more or less appressed pubescence, generally has basal leaves, and has long peduncles, common in L. sellulus. Lupinus sellulus and L. culbertsonii subsp. culbertsonii are sympatric in the Kaweah region.



FIGS. 1-2. Lupinus distributions. 1. Distributions of the subspecies of L. culbertsonii in the Sierra Nevada of California. 2. Distributions of the subspecies of L. cusickii in eastern Oregon and western Idaho.

- 1b. Lupinus culbertsonii subsp. hypolasius (Greene) B. J. Cox, comb. et stat. nov.—L. hypolasius Greene, Leafl. Bot. Observ. Crit. 1:74. 1904. Type: United States: California: Tulare Co.: Farewell Gap, Purpus 5221 (Holotype: ND; Isotypes: MO, UC, US; Photographs: RSA, UMO).
- L. brunneo-maculatus Eastw., Leafl. W. Bot. 3:19. 1941. TYPE: United States: California: Mono Co.: Mammoth Crest, Mammoth Lakes, *Rose* 35373 (Holotype: CAS; Photographs: RSA, UMO).

Plants perennial, stems from a thick woody caudex (to 3 cm in diameter), semi-decumbent to erect, few, caespitose to sprawling, lower stems and branches frequently becoming somewhat woody with age, curving at nodes, producing a zig-zag pattern of growth, somewhat fistulose, mostly with secondary branching at each node, 13-27(34) cm tall, 1.0–2.5 mm in diameter, short puberulent-strigose, approaching hirsute, cauline nodes 3-6; cauline petioles 2.5-8.0(10) cm long, on immature plant basal leaves 6-8 cm long; stipules 6-11 mm long, adnate to petioles 3–7 mm, attenuate; leaflets 5–8, oblanceolate-elliptic, acute to obtuse-rounded and mucronate; the largest 12-23(39) mm long, 3.8-6.0 (7.5) mm wide, length to width ratio 2.67-5.42, av 3.71, sericeous to pilose on both surfaces; peduncles 1.5–8.0 cm long; racemes 2–10 cm long, usually 3-5 cm, diameter 19-25 mm, flowers in 2-7 verticils, 5-15 mm apart; flowers fragrant, 10.0–12.2 mm long, blue with white to yellow sulcus; bracts persistent, 4.0-8.5 mm long, subulate-attenuate, pilose; pedicels 2-3 mm long; calyx bilabiate, often minutely gibbous at the

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base, upper-lip 4.5-6.4 mm long, bilobed, notch 1.0-2.2 mm deep, lower-lip 5.0-7.0 mm long, entire to serrate, lips connate 1.0-1.8 mm, bracteoles persistent, 0.2-1.0 mm long, attached at the sinus or up to 0.5 mm

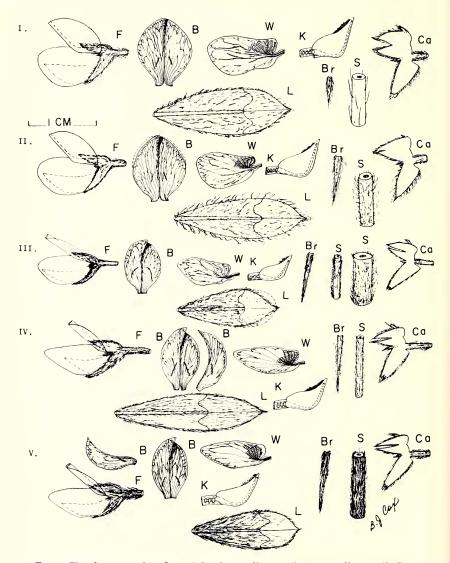


FIG. 3. Floral parts and leaflets of *Lupinus culbertsonii* subsp. *culbertsonii* (I) and subsp. *hypolasius* (II) and *Lupinus cusickii* subsp. *cusickii* (III), subsp. *abortivus* (IV), and subsp. *brachypodus* (V). All parts are drawn to the typical conformation of the structure with the mean value of measurements of a minimum of 25 mature flowers. F =flower; B =banner; W =wing; K =keel; Ca =calyx, inside view, cut open at left lateral sinus; Br =bract; S =stem; and L =av. largest leaflet.

back, strigose-pilose; banner suborbicular to obovate, glabrous, 8.6–10.5 mm long, 6.0–9.3 mm wide, length to width ratio 1.0–1.43, av 1.16, reflexed near the midpoint, reflexed to appressed ratio 0.91–1.20, av 0.99, angle 125–152°; wings 7.9–10.5 mm long, 4.3–6.8 mm wide, length to width ratio 1.44–2.00, av 1.65; keel 2–3 mm wide at the widest point, angle 93–105°, sparsely ciliated along the upper-outer half, most densely near the acumen; ovules 3–4; pods 13–18 mm long, 4.5–5.0 mm wide, densely appressed sericeous; seeds 3–4, 2.6–2.9 mm long, 2.2–2.5 mm wide, 1.1–1.5 mm thick, beige to tan with brown mottling; flowers late July–early August; 2n = 48 (Cox, 1972b); (fig. 3).

DISTRIBUTION: This subspecies often grows in rather dry sandy or granitic soil among boulders or morainal debris in the Sierra Nevada of California, from Tulare Co. to Mono Co., inclusively (fig. 1). It occupies a subalpine to alpine habitat, normally found at elevations of 2900– 3500 meters. Plants are commonly associated with *Pinus murrayana*, *P. albicaulis*, *P. monticola*, *P. contorta*, *Juniperus* sp., *Tsuga mertensiana* and frequently grow at margins of thickets of *Vaccinium* spp.

Although anthesis normally occurs during the latter part of July and first part of August, one collection has been recorded flowering as late as the first of October at 3350 meters elevation on the ridge near Moose Lake, Tulare Co.

The two subspecies of *Lupinus culbertsonii* are morphologically and ecologically distinct. Subspecies *culbertsonii* generally occupies a more mesic habitat than subsp. *hypolasius* and occurs at lower elevations.

The smaller forms of subsp. hypolasius tend to resemble L. lyallii, the largest forms have traits in common with L. sellulus and L. confertus, and one specimen has yellow-green leaflets and stems and the shaggy pubescence typical of L. covillei. A few specimens in an Inyo Co., Calif., population (Alexander & Kellogg 3329 — GH, MO, NY, RM, UC, US) grow in low mats and have silvery leaves much like L. lyallii. Plants from Mono Co. have longer racemes with more verticils than those from elsewhere. Some plants, especially those occurring near Sonora Peak have exceptionally thick woody caudices and stems that are almost entirely glabrous. Lupinus culbertsonii subsp. hypolasius can be readily identified by the rather large orbiculate flowers in lax, verticillate racemes and by the branching, curving (zig-zag) semi-decumbent stems.

2a. LUPINUS CUSICKII S. Wats. subsp. CUSICKII, Proc. Amer. Acad. Arts 22:469. 1887. TYPE: United States: Oregon: Baker Co.: Forks of Upper Burnt River, Cusick 1316 (Holotype: GH; Isotypes: MIN, NY, ORE, POM, UC, US; Photographs: RSA, UMO). — L. aridus var. cusickii (S. Wats.) C. P. Sm., Bull. Torrey Bot. Club 51:303. 1924. — L. lepidus subsp. cusickii (S. Wats.) Detl., Amer. Midl. Naturalist 45:493. 1951 — L. lepidus var. cusickii (S. Wats.) Hitchc., Vasc. Pls. Pacif. NW. 3:315. 1961.

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L. longivallis C. P. Sm., Sp. Lup. 561, 1946. TYPE: United States: Idaho: Valley Co.: Long Valley, *Henderson 3089* (Holotype: DS, Isotype: US).

Plants perennial with profusely branching, caespitose clumps, 12-30 cm in diameter, 6-12 cm tall; stems 1-3 mm in diameter, from thick, branching, woody caudex, soft, silky appressed pubescent to canescent; each stem with 4-15 cauline nodes; cauline petioles 3-7 cm long, often imbricated at the bases; stipules 5.0-13.5 mm long, adnate to the petiole 3-5 mm, subulate; leaflets 6-9, oblanceolate, acute-mucronate, the largest 8-21 mm long, usually 10-12 mm, width 3-5 mm, length to width ratio 2.67-4.2, av 3.08, densely sericeous-pilose (canescent) abaxially, more sparsely so adaxially to glabrous near the apex and midrib; peduncles 1-2 cm long; racemes 2.0-3.5 cm long, dense, capitate to subcapitate; flowers 8.5-9.0 mm long, blue with vellow sulcus; bracts persistent, 5.5-9.0 mm long, subulate-attenuate, short villous; pedicels 3-4 mm long; calyx bilabiate, upper-lip 4-5 mm long, bilobed, notch 2-3 mm deep, lower-lip 4.5-5.5 mm long, entire to serrate, lips connate 1.2-1.5 mm, glabrous within, subappressed sericeous without, bracteoles persistent, 0.5-1.0 mm long, attached at the sinus to 1.0 mm back, short villous to subappressed sericeous; banner elliptic-suborbicular, glabrous, 7.5-8.0 mm long, 5.0-6.0 mm wide, length to width ratio 1.25-1.60, av 1.40, reflexed below the midpoint, reflexed to appressed ratio 1.13-1.50, av 1.40, angle 160-165°; wings 7.0-8.5 mm long, 3.5-4.0 mm wide, length to width ratio 1.75-2.43, av 2.08, claws 1.5 mm long, glabrous; keel 2.0–2.5 mm wide at the widest point, angle 109–118°, ciliated along the upper-outer half of the margin; ovules 2-3; pods 6-11 mm long, 4-5 mm wide, densely short sericeous to subappressed woolly; seeds 1-3, 3.0-3.2 mm long, 2.2-2.5 mm wide, 1.0-1.3 mm thick, beige; flowers in June and July; 2n = 48 (Cox, 1972b); (fig. 3).

DISTRIBUTION: Lupinus cusickii subsp. cusickii is endemic to a narrow region along Burnt River in Baker Co., Oregon, and near Payette Lake in Valley Co., Idaho (fig. 2). The habitat is dry, rocky clay soil in exposed areas that support a depauperate vegetation. The elevation of this habitat is about 1500 meters. Associated plants consist primarily of Artemisia tridentata and Chrysothamnus nauseosus.

This subspecies bears a superficial resemblance to Lupinus carspitosus; however, L. cusickii subsp. cusickii differs in many traits. Unlike L. caespitosus, the stems of subsp. cusickii elongate and branch profusely, forming clumps; inflorescences are more or less capitate, appearing at the same level as the leaflets; flowers are generally larger than those of L. caespitosus, with reflexed banners, and the entire plant is usually canescent with soft appressed pubescence. Frequently, the leaflets are glabrous adaxially at the apex and sometimes along the midrib, a trait held in common with subsp. brachypodus, subsp. abortivus, L. lyallii subsp. minutifolius, and L. saxosus, all of eastern Oregon.

Two variant populations of L. cusickii in Oregon resemble L. aridus

in vegetative patterns. Plants in the Unity Dam population (*Maguire & Holmgren 26732* — GH, MO, NY, UC, US, WS) are approximately 15 cm tall, and are generally somewhat more robust than subsp. *cusickii*. These variants have racemes to 4 cm long, with leaflets to 15 mm long and 5–6 mm wide. The Burnt River population (*Cusick 2543* — GH, MO, NY, ORE, POM, RM, UC, US, WS) consists of plants that are more shaggy, are slightly larger (15–17 cm tall), occur in clumps 15 cm in diameter, have longer cauline petioles (to 9 cm long), have leaflets 20–25 mm long and 6 mm wide, and have internodes more elongated than average.

Plants from Valley Co., Idaho, often have racemes that are more elongated than those of the Oregon populations of this subspecies. On the basis of flower morphology they appear to be referable to subsp. *cusickii* and not to *L. caespitosus* var. *utahensis*, for which they are often misidentified in this geographical region. Although each of these two populations of subsp. *cusickii* is more or less distictive in a number of traits, their morphological and chemical affinity (Cox, 1972a) to subsp. *cusickii* is sufficiently strong to suggest that they must be included in this subspecies.

Both morphologically and geographically, *brachypodus* and *abortivus* are interpreted as being most closely allied to *Lupinus cusickii*. *Lupinus cusickii* subsp. *cusickii* is generally taller, grows in broader clumps, has smaller racemes and shorter petioles, and is more appressed canescent than subsp. *brachypodus*. Subsp. *abortivus* differs by having elongated racemes that extend up to one-third beyond the foliage. Subsp. *abortivus* is also a larger clumped plant with numerous longer, filiform petioles and stems, and the leaflets are longer and more linear than either of the other two subspecies.

2b. Lupinus cusickii subsp. abortivus (Greene) B. J. Cox, comb. et stat. nov. — L. abortivus Greene, Muhlenbergia 8:117. 1912. TYPE: United States: Oregon: Harney Co.: Stinkingwater, 1350 meters, 21 Jun 1896, Leiberg 2353 (Holotype: US; Isotypes: GH, NY, ORE; Photographs: NY, RSA, UMO, US). — L. aridus var. abortivus (Greene) C. P. Sm., Bull. Torrey Bot. Club 51:303. 1924.

Plants perennial, densely caespitose, branching prolifically from a woody caudex into clumps 20–35 cm in diameter, secondary inflorescence branches rise within 3 cm of the base; stems and petioles filiform, height 12–15 cm, stem diameter 1.0–1.5 mm, densely strigose-sericeous to sub-appressed villous-hirsute; cauline petioles 6.0–9.5 cm long, 2–4 cauline nodes above the 8–10 imbricated basal leaves in the first 3 cm above the branching woody caudex; stipules 10–15 mm long, adnate to the petiole 4–8 mm, subulate-attenuate; leaflets 6–7, oblanceolate-elliptic, acute to slightly mucronate, the largest 14–29 mm long, 4.0–6.5 mm wide, length to width ratio 3.11–6.00, av 4.43, densely short villous on both surfaces; peduncles 1.5–3.5 cm; racemes 3–9 cm, tips exceeding foliage

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1–5 cm; flowers densely verticillate, blue to pinkish lavender, 10.0–11.5 mm long; bracts persistent, 7–9 mm long, subulate-attenuate, villous; pedicels 3–4 mm long; calyx bilabiate, upper-lip 4–5 mm long, bilobed, notch 2.0–3.5 mm deep, lower-lip 5.0–6.5 mm long, serrate to tridentate, center tooth 0.3–1.0 mm long, lips connate 1.5–2.0 mm, bracteoles persistent, 0.7–1.0 mm long, attached 1 mm back from sinus, shaggy pubescence; banner oblong-elliptic, glabrous, 8–9 mm long, 4.5–5.5 mm wide, length to width ratio 1.45–1.89, av 1.65, reflexed below the midpoint, reflexed to appressed ratio about 1.7, angle 143–155°; wings, 9.0–10.0 mm long, 4.0–4.5 mm wide, length to width ratio 2.1–2.5, av 2.34, claws 1.5–2.0 mm long, glabrous; keel 2.5–3.0 mm wide at the widest point, angle 107–117°, ciliation from the tip half way back along the upper margins; ovules 2–3; pods 10–13 mm long, 5–6 mm wide, villous to shaggy; seeds 2–3, 2.5 mm long, 2.0 mm wide, 1 mm thick, tan to beige color; (fig. 3).

DISTRIBUTION: Lupinus cusickii subsp. abortivus is known only from the type collection (fig. 2).

2c. Lupinus cusickii subsp. brachypodus (Piper) B. J. Cox, comb. et stat. nov. — L. brachypodus Piper, Bull. Torrey Bot. Club 29:642.
1902. TYPE: United States: Oregon: Malheur Co.: "dry stony bottom of small stream margin of Barren Valley," Cusick 2561 (Holotype: not located; Isotypes: GH, MIN, MO, NY, ORE, POM, UC, US).

Plants perennial, from a thick woody caudex, 8-10 mm in diameter at ground level, branching to 5–6 tufts of approximately 15 cm in diameter; stems 4–12 cm tall, 1–2 mm in diameter, densely strigose to ascending short villous-hirsute pubescence; cauline petioles 2-5 cm long, cauline nodes 1-3; leaves mainly basal, basal petioles 1.5-7.0 cm long; stipules 4-5 mm long, adnate to petioles 1-3 mm, small subulate; leaflets unequal, 5-6, oblanceolate-elliptical, acute, the largest 10-18 mm long, 5-6 mm wide, length to width ratio 2.4-3.1, av 2.8, densely sericeous to villous-hirsute abaxially, more sparsely so adaxially, greener above; peduncles 2-4 cm long; racemes 2.0-5.5 cm long, 2.0-2.3 cm in diameter, usually at the level of the leaflets, not exceeding the foliage by more than 1-2 cm; flower arrangement densely subverticillate; flowers 9.5-11.0 mm long, generally 10 mm long, blue to pinkish with a white sulcus; bracts persistent, 6.5-7.0 mm long, attenuate-subulate, pilose-sericeous to villous; pedicels 2.5-3.5 mm long; calyx upper-lip 4.5 mm long, bilobed, notch 2.5-3.0 mm deep; lower-lip 5.0-5.5 mm long, deeply serrate to tridentate, the center tooth 0.3-1.0 mm long, lips connate 1.5 mm, bracteoles persistent, 1.0-1.5 mm long, sericeous to villous, attached at the sinus; banner elliptical, glabrous, 8-9 mm long, 4.5-6.5 mm wide, length to width ratio 1.38-1.78, av 1.65, not reflexed or semi-reflexed forming approximately 160° angle, wings 8-10 mm long, 3-4 mm wide, length to width ratio 2.29-2.83, av 2.50, claws 1.5-2.0 mm long, glabrous; keel 2.0–2.5 mm wide at the widest point, angle $108-118^{\circ}$, ciliated along the upper margin from the acumen to half the distance back; ovules 2–3; pods 10 mm long, 5 mm wide, silky-villous to woolly; seeds 2–3, 2.5 mm long, 2.0 mm wide, 1.0 mm thick, beige to tan color; flowers in mid-June; (fig. 3).

DISTRIBUTION: Lupinus cusickii subsp. brachypodus has been collected only in eastern Oregon in Grant, Harney, Malheur, and Umatilla counties (fig. 2). The plants are found primarily in arid, rocky stream beds and on mountain ridges. They do not occur in abundance, and they have been collected infrequently. Associated plants are predominantly Artemisia spp. and Chrysothamnus spp.

Subspecies brachypodus generally has capitate racemes like subsp. cusickii, but the flowers are larger, approaching the size and shape of those of L. aridus. The vegetative height and general stature of subsp. brachypodus resemble L. caespitosus var. utahensis, but utahensis usually has elongated, narrower racemes and smaller flowers than the former. The petioles of subsp. brachypodus are mainly basal, unlike the cauline leaves of L. caespitosus var. utahensis. Although the raceme diameter and flower size of subsp. abortivus approximate those of subsp. brachypodus, the former has elongated racemes that surpass the foliage by 1-5 cm, forming larger clumps with more filiform stems and petioles.

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FURTHER EVIDENCE FOR THE SYSTEMATIC POSITION OF PSITTACANTHUS SONORAE (LORANTHACEAE)

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The Mexican mistletoe *Psittacanthus sonorae* (S. Wats.) Kuljt has recently been transferred to *Psittacanthus* from *Phrygilanthus* on the basis of a single character (Kuijt, 1971). This character, the absence of endosperm in the mature seed, is in Loranthaceae unique to *Psittacanthus*, at least under the current circumscription of neotropical genera. I should like to further substantiate this taxonomic transfer by means of some observations on the fruit and seedling. These observations, furthermore, include a number of details in which *P. sonorae* differs from other known *Psittacanthus* species; some of these details seem to represent adaptations to the extremely xerophytic environment of the Sonoran Desert. A comparative basis has been provided by my two earlier articles on *Psittacanthus* (Kuijt, 1967 and 1970).

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